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# Contributions of Benthic Microalgae to Coastal Fishery Yield

Peters and Schaaf (1991) presented a thought-provoking synthesis of ecosystem-level trophic dynamics in eastern U.S. coastal waters. One conclusion was that algal production alone is inadequate to support the existing fish production and, therefore, that considerable vascular plant production is required. Here we provide evidence that coastal algal production is significantly greater than Peters and Schaaf estimated and therefore that little vascular plant production may be required to support the fisheries yield.

The additional algal production is generated by edaphic microalgae (growing on bare or vegetated sediments) and epiphytic microalgae (attached to salt marsh macrophytes and sea grasses). These benthic floras are typically dominated by numerous species of diatoms and blue-green algae, but microscopic green, yellow-green, red, and brown algal species may also be abundant. These highly productive algae are heavily grazed by a host of organisms including nematodes, ostracods, harpacticoid copepods, isopods, amphipods, molluscs, shrimp, and various fish (Brook 1977; Orth and van Montfrans 1984). Many of these grazers, in turn, are important food items for estuarine and coastal marine fishes (Carr and Adams 1973; Feller and Kaczynski 1975; Kjelson et al. 1975; Stickney et al. 1975; Johnson et al. 1990).

Peters and Schaaf (1991: Table 4) estimated annual primary production in coastal waters from New York to Georgia as $25.7 \times 10^{12}$ g organic matter, of which $9.9 \times 10^{12}$ g was attributed to salt marsh plants, $0.8 \times 10^{12}$ g to sea grasses, and $15.0 \times 10^{12}$ g to phytoplankton and benthic algae. Edaphic algal production in salt marshes on the eastern Atlantic Coast can be conservatively estimated as about 25% of the overstory vascular plant production (Pomeroy 1959; Gallagher and Daiber 1974; Van Raalte et al. 1976; Sullivan and Moncreiff 1988). This would add about $2.5 \times 10^{12}$ g organic matter to the total primary production in Table 4 of Peters and Schaaf. Although the data were not included in this 25% additional production, Zimba (1990) estimated that the annual production of subtidal microalgae in bayous, creeks, and embayments of a Mississippi salt marsh was nearly 100 g C/m$^2$. Epiphytic algae on salt marsh plants can produce organic matter at hourly rates (per unit substratum) comparable to those of edaphic salt marsh algae (Jones 1980; Stowe and Gosselink 1985). Because the surface area of the macrophyte substratum is much greater than that of the benthic substratum (Burkholder and Wetzel 1989), this can conservatively add at least another $2.5 \times 10^{12}$ g organic matter to Table 4.

Data for edaphic algal production in sea grass beds are sparse, but a study by Daehnick et al. (1992) indicated that edaphic microalgal production was 130% of the sea grass production in Mississippi Sound, and Pomeroy (1960) estimated benthic microalgal production to be 100% of sea grass production in a Florida study. If we conservatively estimate edaphic algae to be 50% as productive as the overlying sea grass, we add another $0.4 \times 10^{12}$ g organic matter to Table 4. Production of sea grass epiphytes can range from about 20 to 200% of sea grass production (Penhale 1977; Heffernan and Gibson 1983; Morgan and Kitting 1984; Jensen and Gibson 1986). If we conservatively assume an average of 50%, we add still another $0.4 \times 10^{12}$ g organic matter. This added microalgal production thus increases total annual east coast primary production to at least $31.5 \times 10^{12}$ g organic matter, of which 66% is algal production.

In Table 6 of Peters and Schaaf (1991), annual primary production per unit area (PP/A) is given as 500 g organic matter per square meter. However, total production in Table 4 ($25.7 \times 10^{12}$ g organic matter) divided by A from Table 6 ($5.3 \times 10^{10}$ m$^2$) is 485 g/m$^2$, the number used by Peters and Schaaf in subsequent calculations. Insertion of our revised primary production values into their Table 6 would result in an increase in PP/A from 485 to 594 g/m$^2$. Thus, PP/Y, the ratio of primary production (grams organic matter) to fishery yield (grams dry weight) would increase from 179 to 219. Peters and Schaaf (1991) calculated that $C_D$ (cost of detritus, the ratio of starting plant weight to resulting detritus weight) can vary from 1 to 2.4 and that CP* (average cost of producing a unit of fish yield) is between 124 and 179, or from 69 to 100% of the total annual primary production of the east coast system. If all energy in the system is used in the trophic structure, CP = PP/Y. Substitution of 219 for CP in Peters and Schaaf's equation (3) alters their equation (4) to $C_{FF} = 326.9 - 7.76C_D$ ($C_{FF}$ is the cost of producing forage fish). Solving the simultaneous equations (3) and (6) then gives a revised maximum permissive value for $C_D$ of 3.4. With edaphic and epiphytic microalgae considered, $C_D$ thus varies from 1 to 3.4 and CP* from 124 to 217, or 57–100% of the total annual primary production of the east coast system.

By subtraction of the percent of algal contribution to primary production (58%), Peters and Schaaf determined that between 11 and 42% of the net primary production of the system must come from vascular plants. Our revised figures indicate algal production to be at least 66% of the total annual production; thus the system would require at the least 0% and at most 34% of total net production to come from vascular plants. Peters and Schaaf indicated that CP* depends on the value used for $C_D$. If all algal production is used (66% of total PP), then CP* = 143. Thus, $C_D$ must equal or exceed 1.5 for the coastal food web to require the support of vascular plant production. Peters and Schaaf used $C_D = 1.54$ for the model in general.

Another algal resource overlooked by Peters and Schaaf (1991) is the wide variety of benthic macroalgae found on rock outcroppings, wrecks, artificial reefs, jetties and harbor structures, marshes, and sheltered wetlands (Hay and Sutherland 1988; Schneider and Searles 1991). These algae provide yet more substrata for epiphytic algae, and many ephemeral forms (such as *Ulva, Enteromorpha,* and *Ectocarpus*) are directly consumed by fish (Hay and Sutherland 1988). These macroalgae can be highly productive; in North Inlet estuary, South Carolina, Coutinho (1987) estimated net annual macroalgal production as 200 g C/m$^2$ and gross annual production as 315 g C/m$^2$. Finally, there is recent evidence that benthic microalgae in nonvegetated coastal waters can produce considerably greater biomass (as chlorophyll *a*) than the phytoplankton of the integrated overlying water column, even for water depths greater than 100 m (Cahoon et al. 1991; Cahoon and Cooke 1992). This previously unmeasured algal biomass, primarily composed of diatoms, could represent another significant source of algal production helping to support the coastal food web. Vascular plants are a vitally important part of the coastal food web, serving as food items, substrata, cover, and pollutant filters. However, algal production alone is likely great enough to support most of the coastal fisheries yield. Although some species, such as menhaden *Brevoortia* spp., depend greatly upon vascular plant detritus (Lewis and Peters 1984), the majority of the fisheries yield probably relies less on vascular plant production than indicated by Peters and Schaaf (1991). Peters and Schaaf have contributed an important initiative regarding coastal food web research. We recommend that plankton ecologists, limnologists, wetland ecologists, and fishery scientists consider the often overlooked edaphic and epiphytic algae as they construct future food web models. This understudied yet very important group of organisms merits more attention from the scientific community if we are to better understand trophic production and food web dynamics in our aquatic ecosystems.

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Our paper (Peters and Schaaf 1991) summarizes available and relevant information about Atlantic coastal production in a manner that permits quantitative assessment of the size, structure, and functioning of the system. We intended the paper as a conceptual framework upon which to hang working hypotheses. It can be used to ask, for example, "How much additional algal production would be required to eliminate the need for any vascular plant input to the system?" The Comment by Mallin et al. is in this spirit. Because coastal production still is poorly quantified, a point-by-point rebuttal would not be very edifying. We will discuss however, some general considerations that bear on our apparent differences.

Our value of $15 \times 10^{12}$ g may underestimate algal production. Based on the variability in the primary production values we cited and the additional information Mallin et al. provided, however, we are unconvinced the difference is substantial. Published estimates of net primary production vary because of differences in techniques, season, habitat, community, location, and perhaps other factors. We presented the value for annual production of organic matter in open water (350 $g/m^2$) as a "smudgy" average that includes both phytoplankton and benthic algae (i.e., edaphic and epiphytic microalgae and benthic macroalgae). We did not account for edaphic algal production in intertidal marshes, although our annual rate for emergent marsh plants (1,200 $g/m^2$, based on 19 estimates) apparently includes some epiphytic production. Algal contribution to our estimate of marsh production is unknown and may be inconsequential. The importance of production by epiphytic marsh algae is not universally recognized; Stowe and Gosselink (1985) speculated that "The role of the epiphytic community is one of quality production rather than quantity," and Jones (1980) stated that epiphytes "may" be an important source of primary production during some seasons. The average of the two studies within our system that Mallin et al. cite is 220 $g/m^2$ annually. If that value represents all marshes in the system, our estimate of total production could be increased from 25.7 to $27.5 \times 10^{12}$ g. Alternatively, total system primary production would not change if annual open-water production averaged only 310 $g/m^2$. Is this figure too low?

The question is largely rhetorical because of the immense variability of estimates in the literature. Mallin et al. state that "Production of seagrass epiphytes can range from about 20 to 200% of seagrass production." It was about 20% in the only study they cited (Penhale 1977) from within our system. After trying to eliminate estimates that may not be relevant (we eye studies from other areas quite skeptically), we are still left with plenty of conundrums to average. The annual algal production rates we used to obtain the value in our Table 4 vary from about 100 to 700 $g/m^2$ with a 69% coefficient of variation. Our rate was based on an average of 12 published values; when Smayda (1973) gave a range, we used the upper value; to be conservative we rounded the resulting average (322) up to 350. Our answer to our rhetorical question is: No, 310 $g/m^2$ probably is not too low.

A better estimate of primary production will arise when scientists like Mallin et al. carefully summarize information for the entire system. We suspect that variability can be reduced and accuracy increased by greater stratification of estimates—stratification not only by benthic macroalgae, edaphic microalgae, and phytoplankton, as Mallin et al. suggest, but also by substrate, depth, water clarity, and other factors. We hope that our study has begun to instigate this process. So far, we do not see that we seriously underestimated total primary production in the Atlantic coastal system or the relative contributions of emergent marsh plants, sea grass, and algae, the three main producers.

Mallin et al. question our conclusion that 11–42% of the primary production needed to maintain the fishery yield comes from vascular plants. We do not yet regard their estimate of 0–34% to be meaningfully different, especially at the upper limit. If $C_D$ is 2.1 rather than an unrealistic 1.0, their lower value becomes 11% as well.

Mallin et al. seem not to be arguing that emergent marsh plants are unimportant in the food web. Similarly we are not arguing that edaphic and epiphytic microalgae are unimportant. We all agree that considerably more information is needed on all fronts if we are to gain a better understanding of coastal production systems and their relation to fishery yield.

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